NEW MIOCENE BULUNGAMAYINE KANGAROOS (MARSUPIALIA: POTOROIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Nowidgee matrix gen. et sp. nov. and *Ganguroo bilamina* gen. et sp. nov. are described from freshwater Miocene System B limestone at Riversleigh, NW Queensland. Subfamilial diagnosis of Bulungamayinae is emended. The new species indicate that lophodonty was achieved in bulungamayines by a different process from that in balbarines. Similarities in dental morphology between bulungamayines and late Miocene macropodids suggest that Bulungamayinae is ancestral to Macropodidae. ☐ *Riversleigh, kangaroo, balbarines, Bulungamayinae, lophodonty.*

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Rat-kangaroos or potoroids, in the sense of Archer & Bartholomai (1978) and Bartholomai (1978), were unknown in the pre-Pliocene fossil record of Australia until Archer (1979) described *Wabularoo naughtoni* as an enigmatic, lophodont kangaroo from the Riversleigh Local Fauna of the Carl Creek Limestone. Flannery et al. (1982) described *Bulungamaya delicata* from the Carl Creek Limestone and placed it and *W. naughtoni* in the potoroid Bulungamayinae. *Gumardee pascuali*, also from the Carl Creek Limestone was described in the same paper but placed in the Potoroinae. More recent additions to the record of potoroines include *Wakiewakie lawsoni* Woodburne, 1984 and *Purtia mosaicus* Case, 1984, from the Ngapakaldi Local Fauna of South Australia and *Bettongia moyesi* Flannery & Archer, 1987, from Two Trees Site at Riversleigh. Flannery & Rich (1986) described *Gumardee* and indeterminate potoroines from the Tarkarooloo Local Fauna of South Australia.

Archer & Flannery (1985) erected Propleopinae for *Ekaltadeta ima*, a giant rat kangaroo from Gag Site at Riversleigh and Pleistocene and Pliocene species of *Propleopus*. Flannery & Archer (1987) described *Hypsiprimnodon bartholomaii* from the Gag Site at Riversleigh and Flannery & Rich (1986) reported hypsiprimnodontine material from the Tarkarooloo Local Fauna. Palaeopotoroinae Flannery & Rich, 1986 accommodates *Palaeopotorous priscus* from the Tarkarooloo Local Fauna.

The diversity of pre-Pliocene potoroids is such that only 2 of the more recently discovered species have been assigned to existing genera and 3 new subfamilies have been proposed. Of these Bulungamayinae Flannery et al., 1982, has attracted most discussion. Woodburne (1984) and Case (1984) argued that the lophodont bulungamayines *W. naughtoni* and *B. delicata* share characteristics with plesiomorphic macropodids (their macropodines) such as *Dorcopsoides fossilis* Woodburne, 1967, *Dorcopsis* and *Dorcopsulus* and should be included in Macropodidae (their Macropodinae). They also argued a similar placement of *Gumardee*. Flannery et al. (1984) identified synapomorphies which they considered united potoroids in a monophyletic group and defended their placement of bulungamayines and *G. pascuali* within Potoroidae on the basis of several of those derived states. Flannery & Archer (1987a, b) demonstrated that one suggested synapomorphic character, squamosal-frontal contact on the lateral wall of the cranium, is not universal within the group and could no longer be considered as a potoroid synapomorphy. The state of this character is unknown in new bulungamayine material described below.

The new species are similar in size and have similar premolar morphology to that of *B. delicata* and together with that species represent a sequence which reveals much about the evolution of lophodonty within Bulungamayinae.

METHODS

Molar homology follows Luckett (1993), premolar homology follows Flower (1867). Dental descriptive terminology is principally that used by Archer (1984) but with some terms adopted from Szalay (1969) and Ride (1993). In upper molars the term, 'paracingulum' is used to indicate an anterior cingulum bounded laterally by the preparacrista and preprotocrista as indicated in Szalay (1969). Ride used 'precingulum' for this structure. I use 'precingulum' for an anterior cingulum extending lingually from the preprotocrista, following Szalay. This structure was referred to by Ride as the 'anterolingual cingulum'. 'Metacingulum' is used for a posterior cingulum bounded posterolingually by the postmetaconule crista; 'paracrista' and 'metacrista' are used for the lingually directed, loph-forming cristae from the paracone and metacone, respectively. Use of the latter term in this manner is a departure from Szalay who uses 'metacrista' synonymously with 'postmetacrista'. 'Postmetacrista' is used here in the sense of Archer (1984).

Cusp homology of upper molars is that of Tedford & Woodburne (1987), with the posterior buccal and lingual cusps designated as metacone and metaconule respectively, and the cuspule between these as the neometaconule. Suprageneric classification follows Aplin & Archer (1987). Material is housed in the Queensland Museum (QMF). Measurements are in millimetres.

SYSTEMATICS

Superfamily MACROPODOIDEA Gray, 1821
Family POTOROIDAE Gray, 1821
Subfamily BULUNGAMAYINAE Flannery, Archer & Plane 1982, emend. Cooke, 1997

Bulungamayines have a buccally expanded masseteric canal confluent over its length with the inferior dental canal, the common canal penetrating deeply within the dentary below the molar row. The digastric process of the dentary is expanded so that the ventral margin of the dentary is convex below the molar row. I_1 has enamel confined to the buccal surface but extensive on that surface and not confined to the ventral portion as it is in potoroines. Ventral and dorsal enamel flanges are present on I_1. P_3 is elongate with many fine transcristids and a bulbous base. A small tooth, I_2 but which may be a small canine, is just posterior to the dorsal margin of the I_1 alveolus. Molar teeth may be bunolophodont or lophodont as defined by Flannery et al. (1984).

Bulungamayines differ from hypsiprimnodontines and propleopines by having an elongate P_3 whose occlusal margin in lateral view is straight or concave, rather than a plagiaulacoid P_3 with a convex occlusal margin. They differ from potoroines by having much more bulbous premolars, by having an I_2 and a much more extensive area of enamel on the buccal surface of I_1. They differ from palaeopotoroines by lacking a distinct protostylid on M_1.

REMARKS. Type specimens of bulungamayines erected herein are far more complete than those of previously described species and reveal details of anatomical and dental features absent in the holotypes of *Bulungamaya delicata* and *Wabularoo naughtoni*. This additional information forces the above subfamily revision.

Nowidgee gen. nov.

TYPE SPECIES. *Nowidgee matrix* sp. nov.

DIAGNOSIS. Bulungamayine with bunolophodont molars. Upper molars with a large stylar cusp C extending posteriorly to close the buccal end of the interloph region.

ETYMOLOGY. Waanyi (as spoken by Ivy Stinken, formerly of Riversleigh Station) *Nowidgee*, grandmother.

Nowidgee matrix sp. nov.
(Figs 1, 2; Table1)

DIAGNOSIS. As for the genus.

MATERIAL EXAMINED. Holotype QMF30390, from Camel Sputum, Godthelp's Hill, D-Site Plateau. Paratypes QMF19961, 20255, 22761, 30393, 30394, 30395 from Camel Sputum Site, QMF19937, 20069, 20080, 30391 from Wayne's Wok Site, Hal's Hill, D-Site Plateau. Both System B sites (Archer et al., 1989) of Miocene age.

ETYMOLOGY. Latin *matrix*, mother of an animal, refers to its ancestral position.

DESCRIPTION OF HOLOTYPE. Right dentary fragment of most of the horizontal ramus to the level of M_4 and part of the ascending ramus. I_1, P_3 and M_{1-4} preserved. Ascending ramus at about 110° to occlusal plane of molar row. Masseteric canal confluent with inferior dental canal, making it difficult to assess extent of forward penetration of the masseter, but anterior wall of masseteric fossa extending anteriorly to about level of the M_3 protolophid. At this level diameter of common canal not greatly exceeding that of sulcus representing inferior dental canal in posterior, lingual wall of masseteric fossa. This suggests anterior portion of common canal occupied chiefly by vessels associated with dental canal and masseter not passing much more anteriorly than this level. Masseteric fossa buccally expanded with flat surface for attachment of superficial layer of masseter at anteroventral border, extending dorsally on anterobuccal margin of ascending ramus. Ventral margin of horizontal ramus gently convex with lowest point below M_2/M_3. Mental foramen just anterior to P_3, between root of I_1 and dorsal margin of the diastema; much smaller posterior mental foramen ventral to protolophid of M_2. Posteroventrally inclined buccinator sulcus between P_3 alveolar margin and posterior mental foramen. Diastema short, as long as P_3. Damage to I_1 alveolar margin obscuring I_2 or its alveolus (I_2 alveolus in QMF 19937). Mandibular symphysis extending posteriorly almost to level of P_3 posterior margin.

Dentition. Molar row straight in occlusal view, P_3 flexed slightly buccally out of alignment with it. In lateral view molar row concave: occlusal surfaces of M_2 and M_3 lying below line joining occlusal surfaces of M_1 and M_4. Effects of wear on molar teeth progressively less obvious towards posterior of molar row. Molar size increases from M_1-M_3 but M_3 larger than M_4.

I_1 broken at anterior end, depth uniform over preserved length, rising at approximately 20° relative to dorsal margin of horizontal ramus. Enamel confined to buccal side, has both dorsal and ventral enamel flanges, ventral being more strongly developed. Dorsal flange forms occlusal margin. Circular cross-section close to alveolus becoming more elliptical anteriorly.

P_3 blade-like, 50% longer than M_1. Occlusal outline semilunar with straight lingual margin and convex buccal margin. Occlusal crest slightly lingual to midline, flexes lingually at posterior end. Six small cuspids on occlusal margin anterior to longer, posterior cuspid. Transcristids associated with each of 6 minor cuspids and anterior and posterior margins of blade delineated by vertical cristids. Lingual surface of occlusal blade more steeply inclined than buccal.

M_1 almost square in occlusal outline but narrower anteriorly than posteriorly. Protolophid shorter than hypolophid: protoconid closer to midline than is hypoconid. Lingual cuspids taller, more sharply angular and closer to adjacent lateral margin than rounded, buccal counterparts which are also more worn. Lingual surfaces vertical, buccal surfaces more gently sloping. Protolophid formed by metacristid descending buccally from metaconid apex to lingual flank of protoconid. Thick paracristid running anterolingually from apex of protoconid to anterior margin. Short, broad anterior cingulid anterior to anterior face of protolophid, bounded buccally by paracristid, lingually by anteriorly directed premetacristid. Broad precingulid sloping steeply ventrally buccal to paracristid. Sharply-defined postmetacristid curving buccally from metaconid apex, descending to narrow interlophid valley. Anteriorly oriented preentocristid separated from ventral end of postmetacristid by narrow cleft. Cristid obliqua very thick, descending anterolingually from apex of hypoconid to interlophid valley, then inclining buccally to apex of protoconid. Paracristid and cristid obliqua form continuous longitudinal ridge extending from anterior margin to hypoconid. Hypolophid formed by buccal crest from the entoconid descending from entoconid apex and running buccally to meet lingual flank of hypoconid. Posthypocristid descending lingually from hypoconid apex, crossing lingually posterior to buccal crest from entoconid to posterior of entoconid below apex.

M_2 larger and squarer than M_1 with protolophid and hypolophid of about equal length and protoconid and hypoconid in alignment. Similar to M_1 but anterior cingulid longer and broader, precingulid shorter and interlophid valley broader.

M_3 worn in trigonid region but talonid relatively unworn. Crown very similar to M_2 but most structures more clearly defined. Cristid obliqua massive in interlophid region, not much lower than apices of buccal cuspids. Lingual side of interlophid valley more open with greater separation of ventral ends of postmetacristid and preentocristid. Posthypocristid sharply defined crossing posterior surface from hypoconid apex to short, almost vertical postentocristid descending from apex of entoconid. Deep, narrow trench between crest of posthypocristid and buccal crest from entoconid anterior to it.

M_4 unworn. Hypolophid shorter than protolophid. Cristid obliqua originating on anterobuccal face of hypoconid, below apex. Preentocristid and postmetacristid separated only by narrow cleft in interlophid valley. Posthypocristid crest rounded, meeting entoconid much closer to its apex than on anterior molars. Buccal crest from entoconid shorter and less sharply defined.

DESCRIPTION OF PARATYPES.

DENTARY FRAGMENTS. Horizontal ramus not as deep in juveniles as in adults. Posterior mental foramen varies from beneath M_2/M_3, (ho-

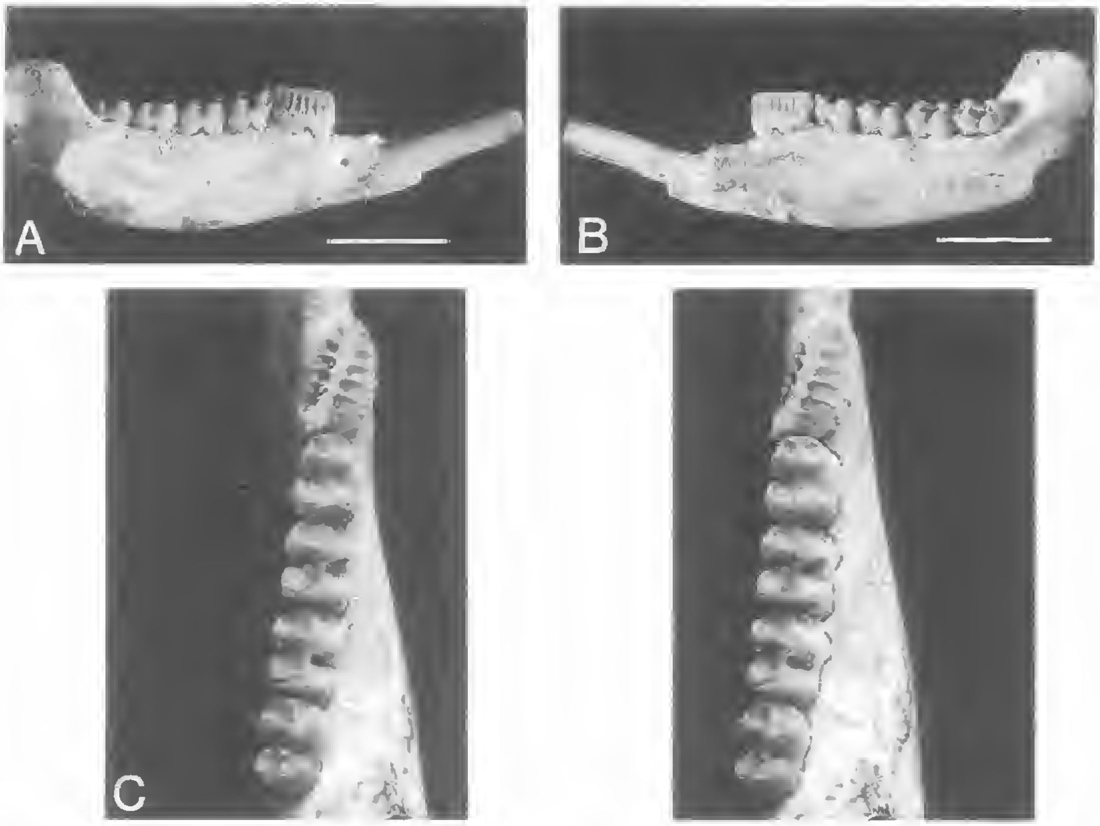

FIG. 1. QMF30390, Holotype, *Nowidgee matrix* sp. nov. A, buccal view; B, lingual view; C, stereopair of occlusal view. Scales = 10mm. AR number is that of the Archer collection, University of New South Wales.

lotype) to as far anterior as beneath hypolophid of M_1. QMF20080 preserves angular process and much of ascending ramus but lacks condyle and coronoid process. Lingual margin of angular process low, aligned with molar row, posterior margin sloping ventrally towards lingual end. Pterygoid fossa triangular in dorsal view, buccal margin slightly undercutting base of ascending ramus. Mandibular foramen a narrow, vertically oriented ellipse, opening to very short posterior portion of inferior dental canal opening via masseteric foramen to masseteric fossa. Masseteric foramen just visible when masseteric fossa viewed from buccal side. Molar row ventrally concave. Ascending ramus at about 113° to line of a straight edge laid on molar row.

LOWER DENTITION. dP_2 and dP_3 preserved in QMF20080 and 20063, detached dP_3 available for QMF30392. dP_2 (Fig. 2A) short, blade-like, with bulbous base tapering anteriorly and posteriorly. Occlusal margin straight, relatively horizontal, with 4 small cuspids anterior to longer, posterior cuspid overhanging posterior base of tooth. Fifth cuspid incompletely differentiated from large, posterior cuspid in QMF20080. Transcristids associated with each of 4 anterior cuspids. Posterior, buccal face of crown abutting anterior lingual face of dP_3.

dP_3 (Fig. 2A) narrower anteriorly than posteriorly, dominated by massive, laterally compressed protoconid, the tallest cuspid on tooth. No distinct metaconid. Paracristid anterolingually directed, descending to paraconid on anterior margin. Cristid descending steeply from paraconid apex to crown base on buccal side of anterior margin. Cristid descending posterior face of protoconid to interlophid valley. Paraconid, paracristid and protoconid form blade-like crest complementing that of dP_2. Entoconid taller, more angular than hypoconid. Cristid obliqua running anterolingually from apex of hypoconid, crossing interlophid valley and ascending buccal flank of protoconid. In QMF20069 and QMF30392 a short, buccally-

FIG. 2. Paratypes of *Nowidgee matrix* sp. nov. A, stereopair of occlusal view of QMF20080, right dentary fragment with dP_{2-3}, M_{1-3}, (M_4). B, stereopair of occlusal view of QMF30395, right maxillary fragment with P^3, M^{1-4}. Visible number is that of the Archer collection, University of New South Wales.

directed protostylid crest joining protoconid apex to a prominence (reduced protostylid), contacted by anterior end of cristid obliqua. Sharp preentocristid running to interlophid valley from entoconid apex. Buccally-directed crest from entoconid descending steeply buccally from entoconid apex to about midline of tooth. Posthypocristid descending lingually from hypoconid apex to shorter postentocristid ascending to entoconid apex.

P_3 in QMF19937 and 30394 resembles holotype but with seventh minor cuspid, imperfectly differentiated from long posterior cuspid of occlusal crest. Seventh minor cuspid more clearly differentiated in P_3's removed from crypts in QMF20080 and QMF30392.

Except for QMF19961 in which anterior molars very worn, molar teeth in paratypes less worn than those of holotype. Molar morphology among paratypes very similar to holotype.

TABLE 1. Dental parameters for type specimens of *Nowidgee matrix* sp. nov.

Number	P2 l	P2 w	P2 h	P2 tcn	P3 l	P3 w	P3 h	P3 tcn	dP3 l	dP3 aw	dP3 pw	M1 l	M1 aw	M1 pw	M2 l	M2 aw	M2 pw	M3 l	M3 aw	M3 pw	M4 l	M4 aw	M4 pw
F30390					6.0	3.2	3.6	6				3.9	2.8	2.96	4.1	3.1	3.2	4.1	3.2	3.0	4.2	3.1	2.8
F20080	3.9	3.4	3.4	4					3.4	2.2	2.6	3.8	2.4	3.0	4.0	2.5	2.9	3.7	2.6	3.0			
F20069	3.3	2.7	3.0	4	6.4	3.2	3.5	6	3.4	2.0	2.3	3.8	2.7	2.7	4.2	3.1	2.8						
F30391												3.9	2.6	2.8	3.8	3.0	3.0						
F19937					6.4	3.6	4.5	6															
F22761												3.3	1.6	2.0	3.6	2.3	2.3						
F30392									3.4	2.2	2.3	3.6	2.6	2.5	4.2	2.5	2.9	4.2	2.5	2.9			
F19961												4.2	2.5	2.5	4.2	3.1	3.1	3.9	2.8	2.8	3.8	2.7	2.5
F20255																		4.5	3.4	3.1	4.1	3.0	2.8
F19991																		3.9	3.1	3.0	4.1	3.1	
F30393									3.3	2.4	2.5	3.7	2.5	2.5									
F30394					7.1	3.2	3.8	6				4.0	2.2	2.6	3.8	2.9	3..0	4.0	3.1	3.0	4.0	2.9	2.7
MEAN	3.6	3.1	3.2	4	6.5	3.4	3.9	6	3.4	2.2	2.4	3.8	2.4	2.6	4.0	2.8	2.9	3.5	3.0	3.0	4.0	3.0	2.7
SD	.4	.5	.3	0	.5	.3	.5	0	.1	.2	.2	.3	.4	.3	.2	.3	.3	1.5	.3	.1	.2	.2	.1
F30395					7.6	-	3.9	6				4.1	3.8	3.7	4.0	4.2	4.0	4.0	4.1	3.6	3.7	3.4	2.7

2) Maxillary fragment. QMF30395 occludes extremely well with dentary fragment, QMF30394 found in close proximity. Preserves buccal surface of maxilla from diastemal region to masseteric process, including ventral margin of infraorbital foramen, suborbital shelf, alveolar process containing entire cheek tooth row and very narrow portion of palatine wing. Masseteric process of no more than a ventral prominence separated from alveolar process by short, narrow sulcus. Maxillary foramen of infraorbital canal at anterolingual corner of triangular suborbital shelf of maxilla, numerous smaller foramina within ventral margin of foramen. Infraorbital foramen dorsal to midpoint of P^3.

UPPER DENTITION. (Fig. 2B). Molar row slightly convex in lateral view, occlusal edge of P^3 aligned with buccal margin of molar row which curves slightly lingually anteriorly. Molar size increasing from M^1 to M^3; M^4 markedly smaller than M^3.

P^3 almost twice length of M^1, lingual margin damaged, buccal margin convex for 2/3 length, becoming concave for remainder. Occlusal margin anteroposteriorly straight, on midline of tooth. Six small cuspules on margin, succeeded by larger, posterior cuspule which has strong lingual ridge associated with its base.

M^1 with straight anterior and buccal margins and convex lingual and posterior margins. Anterior width greater than posterior width but protoloph and metaloph of about equal length. Low crowned with lingual cusps more massive and more rounded than buccal counterparts. Buccal cusps closer to lateral margin of the tooth: buccal surfaces of crown almost vertical, lingual surfaces sloping. Narrow lingual cingulum reaching from anterior, lingual base of protocone to base of metaconule. Protoloph formed by strong paracrista directed lingually from paracone apex and which meets buccal flank of protocone below apex. Preparacrista runs anteriorly from paracone apex to anterior margin and is continuous with anterior margin of paracingulum bounded laterally by preparacrista and anterobuccally inclined preprotocrista which meets anterior margin anterior to junction of paracrista with protocone. Very large stylar cusp C closing interloph valley on buccal side. Postparacrista and premetacrista reaching floor of interloph valley from respective cusp apices, but not united. Postprotocrista strongly developed but worn in interloph region, contacting metaloph crest just buccal to apex of metaconule. Prominent neometaconule at about centre of metaloph with rounded crista running posteriorly for about half height of metaloph. Postmetaconule crista buccally inclined on posterior face of metaconule, crossing posterior base of metaloph as margin of strong metacingulum, contacting posteriorly directed postmetacrista at base of metacone.

M^2 considerably wider anteriorly than posteriorly, occlusal outline more bluntly triangular. Crown differing from M^1 in: lingual cingulum continuous with precingulum extending anteriorly across base of protocone to anterior end of preprotocrista; stylar cusp C slightly more anteriorly positioned on buccal flank of paracone and does not completely close buccal end of interloph valley; neometaconule and its crista less obvious. M^3 very similar to M^2 but lingual cingulum not as sharply defined, stylar cusp C smaller, postparacrista and premetacrista unite to form continuous centrocrista. M^4 much smaller than anterior molars. Metaloph markedly shorter than protoloph. Lingual cingulum separated from precingulum, all cristae sharply defined. Metaconule lower; no neometaconule or stylar cusp C.

REMARKS. *Nowidgee matrix* is similar in size to *Bulungamaya delicata* but has bunolophodont, rather than lophodont molars. Its bunolophodont lower molars resemble those of *Purtia mosaicus*, but molar occlusal outline in *N. matrix* is more rectangular, rather than square as in *P. mosaicus*. P_3 of *N. matrix* differs from that of *P. mosaicus* in having 6-7 rather than 8 transcristids and, while having a bulbous base, lacks the distinct lateral cingulids of *P. mosaicus*. It differs from *P. mosaicus* in having an I_1 which has both ventral and dorsal enamel flanges and in having enamel which, while confined to the buccal surface, extends over that surface rather than being confined to its ventral portion as in *P. mosaicus* and other potoroines. Lower molars of *N. matrix* are similar to lower molars from the Tarkarooloo Local Fauna assigned by Flannery and Rich (1986) to *Gumardee*, but differ from them by being smaller in size. P_3 of *N. matrix* has 6-7 transcristids, apparently many fewer than the P_3 from the Tarkarooloo *Gumardee*, in which the posterior half, the only portion recovered, has 6 transcristids.

Among potoroids a dorsal enamel flange on I_1 is confined to *Hypsiprimnodon*, *Potorous*, bulungamayines (Flannery et al., 1984) and *Milliyowi bunganditj* (Flannery et al, 1992). *N. matrix* differs from *Hypsiprimnodon* by having permanent premolars which are elongated with horizontal or concave occlusal margins rather than plagiaulacoid with convex occlusal margins, by failure to retain dP_2 after the eruption of P_3 and by having less disparity between the lengths of protolophid and hypolophid on M_1. *N. matrix* differs from *Potorous* by having lower molars in which the buccal cuspids are positioned lingual to the adjacent lateral margin with the result that buccal crown walls are not as steep as in *Potorous*. *N. matrix* differs from the similarly strongly bunolophodont early Pliocene *Milliyowi bunganditj* in having a strongly developed stylar cusp C on M^1 (absent in *M. bungantij*) and in lacking branches of the transcristids of P_3.

The resemblance of the I_1 dorsal enamel flange to that of macropodids is suggestive of a similarly macropodid-like cutting action during occlusion of upper and lower incisors, an unusual feature in an animal with bunolophodont molars similar to those of omnivorous potoroids in which incisors perform a more forcipulate function.

The posteroventrally inclined buccinator sulcus in *N. matrix* was termed the 'labial groove' by Stirton (1963) who noted it in *Protemnodon* and other macropodids. Woodburne (1967) reported a similar structure in *Hadronomus puckridgi*. Where such a sulcus occurs among macropodids and other potoroids it is usually closer to and parallels the alveolar margin.

The reduced cuspid on the buccal flank of the large, central cuspid of the dP_3 trigonid which is linked by ridges to the apex of that cuspid and to the cristid obliqua, is interpreted herein as a reduced protostylid since it occurs in the corresponding position and bears the same relationship to the cristid obliqua as do similar structures on M_1 of other species, i.e., the protostylid crest of *Wururoo dayamayi* Cooke, this volume, the discrete protostylid of *Nambaroo saltavus* Flannery & Rich, 1986, and the protostylid of *Palaeopotorous priscus*. The dominant trigonid cuspid lingually adjacent to the protostylid on dP_3 of *N. matrix* and from which the paracristid arises is thus the protoconid and the metaconid has been lost. The loss of the metaconid of dP_3 may be, as suggested by Ride (1993), the result of a need to supplement the shearing crest of dP_2 which is shorter than the permanent premolar in this species.

Apart from the discrete protostylid rather than a protostylar ridge, the holotype tooth of *P. priscus*, designated as M_1 (their M_2) by Flannery & Rich (1986), bears strong similarities to dP_3 in paratypes of *N. matrix*. Undescribed Riversleigh bulungamayines also have a protostylar ridge on dP_3 and a posterobuccally inclined protolophid similar to *P. priscus*. Since the latter character does not occur on molar teeth of plesiomorphic species such as *N. matrix* which have otherwise similar bunolophodont molars, it is suggested that the holotype tooth of *P. priscus* is dP_3 rather than M_1. If this is the case, *P. priscus* must still be regarded as more plesiomorphic than *N. matrix* in view of the discrete protostylid on this tooth, but other differences in this tooth, or in molars referred to this species, are here regarded as insufficient to warrant the erection of a new subfamily. Subfamilial affinities of the species remain uncertain: its bunolophodont molar morphology suggests it may represent either a plesiomorphic potoroine or bulungamayine. However, the discrete protostylid on the holotype (dP_3) is plesiomorphic and the species may prove to be basal to both these taxa.

Lower molars in *N. matrix* are suitable to be ancestral to *B. delicata*. Lophids in *N. matrix* are clearly formed by transverse cristids extending buccally from the lingual cuspids. The posterior cingulid is enclosed by the posthypocristid which sweeps lingually posterior to the hypolophid and low on the crown before linking to the postentocristid on the posterior of the entoconid. In *B. delicata* the protolophid is formed in a manner similar to that of *N. matrix* but joins the protoconid closer to its apex. The posthypocristid is more elevated on the crown, more transversely oriented and links to the entoconid much closer to the entoconid apex. The buccally oriented crest from the entoconid is reduced in length and in prominence, the posthypocristid having formed a neomorphic hypolophid.

In the low-crowned upper molars of *N. matrix*, lophs are formed by cristae extending lingually from the buccal cusps, upper and lower molars showing reversed symmetry in this respect. Longitudinal crests, notably the pre- and postprotocrista are emphasised, as they are in *Gumardee pascuali*. Strong longitudinal cristae characterise bunolophodont upper molars as defined by Flannery et al. (1984) who suggested that these might work in a different way to lophodont molars in which transverse rather than longitudinal cutting crests are emphasised.

In some undescribed plesiomorphic Riversleigh balbarines (pers. obs.) stylar cusps C and D or their stylar crests are present in the interloph region. *N. matrix* retains only stylar cusp C and lacks any trace of stylar cusp D. While both balbarines and bulungamayines are likely to be derived from bunolophodont ancestors, the absence of stylar cusps other than C in what is an extremely plesiomorphic bulungamayine, suggests that loss of other stylar cusps had already occurred in the bulungamayine ancestor which must in this aspect at least, be more derived than that of balbarines.

Ganguroo gen. nov.

TYPE SPECIES. *Ganguroo bilamina* sp. nov.

DIAGNOSIS. Bulungamayines with lower molars which are completely bilophodont, lacking any trace of a buccally-directed crest originating from the entoconid and anterior to the hypolophid.

REMARKS. *Ganguroo* gen. nov. differs from all potoroines, hypsiprimnodontines and propleopines by having bilophodont lower molars. It differs from all macropodines and sthenurines by having a combination of: low-crowned molars; finely-ridged, elongate premolars; a deeply penetrating masseteric canal confluent over its length with the inferior dental canal. It differs from all balbarines by having the elongate, finely-ridged premolars referred to above, lacking a transversely compressed trigonid on M_1 and in lacking a posterior cingulid on lower molars.

ETYMOLOGY. Waanyi (as spoken by Ivy Stinken, formerly of Riversleigh Station) *gangu*, grandfather and 'roo' is a common Australian diminutive for kangaroo.

Ganguroo bilamina sp. nov.
(Fig. 3, Table2)

DIAGNOSIS. As for the genus

MATERIAL EXAMINED. Holotype QMF19915 from Wayne's Wok, Hal's Hill' D-Site Plateau. Paratypes QMF19591, 18810, 19814, 19835, 30398, 30399 from Wayne's Wok Site; QMF19868, 19870, 19966, 30400 from Camel Sputum Site, Godthelp's Hill; QMF19642, 20293, 30396, 30397 from Upper Site. Godthelp's Hill; QMF19988 from Mike's Menagerie Site, Godthelp's Hill; QMF23777 from Bites Antennary Site, eastern part of D Site Plateau. All System B, Miocene sites (Archer et al., 1989).

ETYMOLOGY. Latin *lamina*, blade; refers to the bilophodont lower molars.

DESCRIPTION OF HOLOTYPE. Left dentary including horizontal ramus, most of angular process and part of ascending ramus. I_1, P_3 and M_{1-4} preserved. Ventral margin of horizontal ramus strongly convex, deepest below protolophid of M_3, distinct digastric prominence on the ventral margin at this point. Diastema relatively short, less than 20% of length of cheek tooth row. Slender I_1 almost horizontal with dorsal occlusal margin well below plane of cheek tooth row. Alveolus for very small I_2 on dorsal margin of diastema just posterior to margin of I_1 alveolus. Mental foramen close to dorsal margin of diastema below anterior margin of P_3, 2 very small posterior mental foramina more posteriorly, 1 below hypolophid of M_2, the other below protolophid of M_3. Very shallow sulcus for attachment of buccinator muscle sloping diagonally ventrally on buccal surface below M_1-M_2. Ascending ramus at about 105° to line of a straight edge laid across high points of occlusal surfaces of cheek tooth row. Since tooth row concave dorsally, such a line contacts posterior of P_3 and hypolophid of M_4. Buccal margin of masseteric fossa straight with flat area for attachment of parts of superficial layer of masseter extending anteroventrally. Masseteric canal and inferior dental canal confluent anterior to large masseteric foramen. Diameter of foramen and anterior constriction of common canal suggest insertion of deep layer of masseter unlikely to have reached much more anteriorly than M_3. Posterior to masseteric foramen inferior dental canal very short: masseteric foramen almost overlapped by mandibular foramen. Lingual margin of angular process aligned with molar row. Wide, shallow basin of pterygoid fossa overhung buccally by remaining anterior portion of ascending ramus. Mandibular symphysis decreases in height posteriorly, extends to level of posterior margin of P_3.

Dentition. Cheek tooth row anteroposteriorly straight; P_3 flexed slightly buccally out of alignment. In lateral view occlusal margin of P_3 above that of molars. Molars low crowned, bilophodont, no trace of any buccally-directed crest associated with the entoconid. Molar size increases from M_1 to M_3; M_4 is smaller than M_3.

I_1 long and slender with low dorsal and ventral enamel flanges. Dorsal and ventral margins almost horizontal for most of length before latter converges on former at anterior end. Enamel confined to buccal surface. Cross section circular close to alveolar margin, triangular anteriorly, resulting from development of rounded, longitudinal ridge central to lingual surface.

P_3 elongate, blade-like with mostly horizontal occlusal margin serrated over most of length anterior to large, posterior cuspid taller than rest of tooth. Serrations formed by 6 minor cuspids, each with associated transcristids, most posterior of these least distinct and shortest. In occlusal view crown base tapering anteriorly and posteriorly to rounded margins. Buccal margin convex, lingual margin relatively straight. Lingual base of crown bulbous adjacent to central region of occlusal blade, forming poorly-defined, rounded lingual cingulid. Occlusal margin following midline but posterior cuspid flexed lingually. Cristid descending anteriorly from apex of most anterior cuspid to crown base and posterior margin delineated by similar but shorter cristid descending from posterior cuspid.

M_1 subrectangular in occlusal outline, narrower anteriorly than posteriorly. Lingual walls of crown subvertical, buccal side sloping more gently. Tooth worn, more wear on buccal side. Wear facet on posterior of metaconid and breaches in enamel of protoconid, hypoconid and entoconid. Metaconid taller, more angular than protoconid which has been reduced in height by wear. Sharply defined crest of protolophid descending buccally from apex of metaconid to that of protoconid. Short paracristid running anteriorly from base of protoconid to anterior margin. Steeply descending enamel ridge on anterior margin buccal to paracristid, forming margin of short precingulid. Broad anterior cingulid enclosed between paracristid and premetacristid which runs between metaconid apex and anterior margin. Sharp postmetacristid descending posteriorly from metaconid apex to interlophid valley, meeting similarly well-defined preentocristid running anteriorly from apex of the entoconid. Cristid obliqua worn, running anterolingually on anterior face of hypoconid before turning anteriorly across interlophid valley, meeting posterior face of protolophid lingually adjacent to protoconid base. Entoconid taller than hypoconid which is more worn. Crest of hypolophid crossing from posterior of hypoconid apex to meet entoconid apex centrally. Postentocristid descending posterior face of entoconid but no other ornamentation of posterior face of hypolophid. M_2 similar in outline to M_1 but slightly larger and less worn. Metaconid taller than protoconid but hypoconid and entoconid subequal in height. Postmetacristid and preentocristid not uniting in interlophid valley. M_3 largest of molars, unworn, with all cuspids about equal height; lingual cuspids with more angular apices than buccal cuspids. M_4 damaged, lacking protoconid and most of anterior margin. Hypoconid taller than entoconid; no postentocristid.

DESCRIPTION OF PARATYPES. Condyle preserved in QMF19814, 19870, 19810 and 30396. In QMF19870 and 19814 is transversely elongate with rounded posterior margin. In QMF30396 condyle has more circular outline. That of

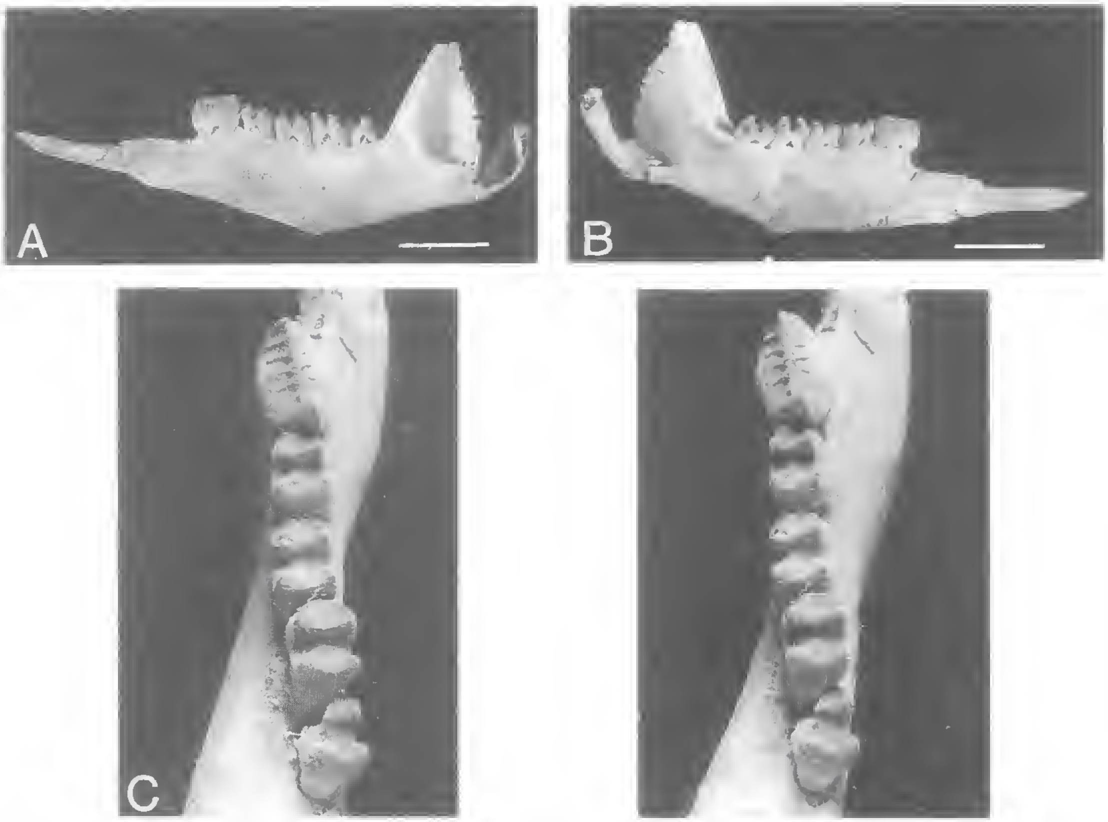

FIG. 3. QMF19915, Holotype of *Ganguroo bilamina* sp. nov. A, buccal view; B, lingual view; C, stereopair of occlusal view. Scales = 10mm.

QMF19810 slightly damaged lingually but similar to, although somewhat smaller than, that of QMF19870 and QMF19814. Differences in shape possibly age related since QMF30396 is from a subadult animal, indicated by incompletely erupted P_3. Height of condyle above plane of molar row varies from 7mm in QMF 19870 and QMF30396 to 11mm in QMF19810, variation possibly being size related. Angle of ascending ramus relative to plane of molar row varies 120° (AR12517)–108° (QMF18814).

Digastric process on ventral margin of horizontal ramus apparently variable within species: QMF19814 level of development comparable to that of holotype, but other paratypes show lesser or no such development. Number of posterior mental foramina also variable: most paratypes have only one such foramen, consistently located below M_2, but none present in QMF30398 while two present in QMF30400 and QMF19966. QMF19988 has number of smaller foramina accessory to mandibular foramen and also has sulcus for vessels of inferior dental canal on lingual wall of masseteric fossa. Posterior portion of inferior dental canal between masseteric foramen and mandibular foramen longer in AR12517 than in holotype and most other paratypes. QMF30400 and QMF19988 have direct opening via single foramen from pterygoid fossa into masseteric fossa with no intervening canal (the condition usual among extant macropodoids).

Damage to ventral margin of horizontal ramus reveals extent of anterior insertion of masseter, in QMF19868 and QMF20293 it reaches level of M_2 hypolophid, but only to level of M_3 hypolophid in QMF30397.

DENTITION. dP_2 and dP_3 in QMF19835, 23777. dP_2 small, blade-like with rounded anterior and posterior margins, strongly convex buccal margin and straight lingual margin. Occlusal crest serrated over much of length anterior to large posterior cuspid overhanging posterior base of crown. QMF19835 has 3 small cuspids in serrated region, each with associated transcristids; 4

TABLE 2. Dental parameters for type specimens of *Ganguroo bilamina* sp. nov.

Number	I_1 l	I_1 w	P_2 l	P_2 mw	P_2 h	P_2 tcn	P_3 l	P_3 mw	P_3 h	P_3 tcn	dP_3 l	dP_3 aw	dP_3 pw	M_1 l	M_1 aw	M_1 pw	M_2 l	M_2 aw	M_2 pw	M_3 l	M_3 aw	M_3 pw	M_4 l	M_4 aw	M_4 pw
F19915	11.6	2.2					5.9	3.3	3.9	6				3.7	2.4	2.6	3.7	2.7	2.8	3.7	2.6	2.6	3.8	-	2.6
F30400																	3.9	2.8	2.9	3.7	2.8	2.8	3.8	2.8	2.7
F23777			4.2	2.5	3.1	3					3.5	2.0	3.3	3.6	2.8	3.0									
F19868	10.9	2.1					5.9	3.1	3.7	5							3.8	2.9	2.8	3.8	2.9	2.9			
F19870											4.2	2.6	2.8	4.0	2.8	3.0	3.8	3.1	3.1	4.0	2.9	2.8			
F19966							5.9	3.1	3.9	6	3.4	2.6	2.8	3.8	2.8	3.0	3.9	3.1	2.9	3.9	3.0	2.7			
F19988																			2.8	3.8	2.8	2.8	3.6	2.9	2.5
F30396		1.7					5.3	2.4		6				3.4	2.6	2.6	3.7	2.7	2.7	3.9	2.9	2.7			
F30397							6.3	3.1	3.7	7				3.5	2.3	2.5	3.9	2.7	2.8	3.9	2.9	2.8	3.9	2.7	2.5
F19642							5.6	2.3	3.9	6				3.5	2.1	2.4									
F20293																	4.1	3.0	3.0	3.9	3.0	2.9	3.9	2.9	2.9
F30399							6.2	2.8	3.6	7				3.5	2.2	2.7	3.5	2.5	2.9	3.6	2.7	2.8	3.8	2.7	2.7
F30398							6.1	3.0	3.5	6				3.5	2.6	2.7	3.6	3.0	2.9	3.8	3.0	2.8	3.5	2.8	2.3
F19591																				3.9	3.2	2.7			
F19810														3.6	2.6	2.6	3.8	2.8	2.8	3.8	2.7	2.9	3.7	2.8	-
F19814							5.9	3.2	3.7	6				3.6	2.5	2.8	3.7	2.6	3.0						
F19835			3.4	3.0	3.6	4	5.7	2.8	4.0	5	2.9	2.3	2.3	3.1	2.5	2.7									
MEAN	**11.3**	**2.0**	**3.8**	**2.8**	**3.4**	**3.5**	**5.9**	**2.9**	**3.8**	**6**	**3.5**	**2.4**	**2.8**	**3.6**	**2.6**	**2.7**	**3.7**	**2.9**	**2.9**	**3.8**	**3.0**	**2.8**	**3.7**	**2.9**	**2.6**
SD	4.9	.3	.6	.4	.4	.7	.3	.3	.2	.7	.5	.3	.4	.2	.4	.2	.4	.3	.1	.3	.3	.1	.3	.4	.2

such cuspids in QMF23777. Anterior and posterior margins of crown delineated by vertical cristids descending from ends of occlusal crest. Occlusal crest runs slightly lingual to midline, lingual surface of crown more steeply inclined than buccal.

dP_3 better preserved in QMF23777 and used as basis for description below. Crown base roughly rectangular in occlusal outline, narrowing somewhat anteriorly. Protolophid extremely laterally compressed, inclined posterolingually, dominated by tall protoconid with thick, rounded protostylid crest descending its buccal flank. Metaconid cannot be distinguished from protoconid. Prominent paracristid (less so in QMF19835) runs anteriorly to tall paraconid (shorter in QMF19385) on anterior margin. Paraconid, paracristid and protolophid form blade-like crest complementing that of dP_2. Vertical cristid descends from posterior margin of protolophid crest to interlophid valley and is contacted by anteriorly directed preentocristid in QMF19835, but not in this specimen. Hypolophid transversely oriented, concave in posterior view. Cristid obliqua runs anterolingually on anterior face of hypoconid, turning anteriorly across interlophid valley and contacting protostylid crest. No ornamentation on posterior face of hypolophid.

P_3 in most paratypes closely resembles that of holotype but QMF30399 has 7 minor cuspids rather than 6.

Molar morphology very similar to that of the holotype although variable postentocristid between different specimens and between different teeth in single specimens.

DISCUSSION

The horizontal orientation of I_1 is similar to that in macropodines in which there is considerable ventral flexion of the rostrum, necessary to bring upper and lower incisors into occlusion and there would presumably be a corresponding flexion of the rostrum in this species. dP_3 is very similar to that of *N. matrix* but is more derived in that the reduced protostylid of *N. matrix* is here further reduced to a protostylid crest. Molars in this species are more derived than in either *N. matrix*, *B. delicata* or *Wabularoo naughtoni* because they are lophodont.

N. matrix, *B. delicata* and *G. bilamina* represent stages in an evolutionary sequence in which a bunolophodont, omnivorous ancestral form is changed to that of a lophodont herbivore (Fig. 4). Hypolophid morphology is particularly informative in this respect. As discussed earlier, a neomorphic hypolophid has been developed in *B. delicata* by elevation of the posthypocristid on the crown and directing the posthypocristid more transversely. Hypolophid morphology in *W. naughtoni* closely resembles that of *B. delicata*. The bunolophodont origin of this morphology is indicated by the reduced buccal crest from the entoconid anterior to the new hypolophid, representing the remnant of the original hypolophid crest. No trace of this crest is evident in *G. bilamina*, the neomorphic hypolophid crest being formed entirely by the elevated, transverse posthypocristid as indicated by the presence of a postentocristid on the posterior face of the entoconid. Loss of the buccally-directed crest from the entoconid represents a subtle change in morphology between *N. matrix* and *G. bilamina* but a highly significant apomorphy.

The evolutionary series represented by these bulungamayine taxa demonstrates that lophodonty evolved independently twice among Oligocene-Miocene kangaroos - once in balbarines in a process which seems to have been essentially that proposed by Flannery & Rich (1986) and once among bulungamayines using the mechanism proposed above. While Flannery (1989) suggested that balbarines were ancestral to macropodines and sthenurines, the similarity of premolar and molar morphology of derived bulungamayines such as G. *bilamina* to that of the later Miocene macropodids from Alcoota is greater than that of more derived balbarines such as *Balbaroo* in which on M_1 there is still considerable lateral compression of the protolophid and little development of the anterior cingulid. The premolar of balbarines is also much shorter than that of bulungamayines and the plesiomorphic Alcoota macropodids (Cooke, 1997).

Lower molar morphology of *G. bilamina* has strong similarities to that of the much larger *Hadronomus puckridgi* Woodburne, 1967 from Alcoota which Murray (1991) regarded as a plesiomorphic sthenurine. Both species are low-crowned and bilophodont, have long anterior cingulids, have M_1 protolophids which are not laterally compressed and lack posterior cingulids, although *Hadronomus* has a bulbous base to the hypolophid. *Hadronomus* also has an elongate premolar, resembling in that respect the premolar of bulungamayines, but that of *Hadronomus* is more coarsely serrated than that in any of the known bulungamayine species and bears well developed lingual and buccal cingula, not present in bulungamayines. However, paratypes of *N. matrix* show variable differentiation of minor cuspids and transcristids on P_3, indicating some lability in degree of serration of the occlusal margin of this tooth in bulungamayines. The bulbous base of the bulungamayine P_3 could serve as an adequate precursor of lateral cingula (a lingual cingulum is poorly developed on P_3 of *G. bilamina*). The premolar of all known balbarines is in contrast a shorter, more plagiaulacoid tooth.

Similarities also exist between dental morphology in *G. bilamina* and in *Dorcopsoides fossilis*, also from Alcoota. While this species was originally included within Potoroidae, Bartholomai (1978) placed it in Macropodinae. Both species have elongate premolars. Lateral cingula are lacking in P_3 of *Dorcopsoides* while a lingual cingulum is poorly developed in that of *G. bilamina* and there are again differences in serration and transcristids between the two species.

dP_3 in *N. matrix* and *B. bilamina* has some similarity with that of *Dorcopsoides* in that the metaconid is reduced or absent in each. Woodburne (1967) also noted the 'fused protoconid and metaconid' of dP_3 in *Dorcopsoides* and 'a short posterolabial crest ... which turns abruptly posteriorly before descending into the transverse valley and continues posterolabially up the anterior face of the hypoconid'. This crest may be homologous with the protostylid crest which is linked to the cristid obliqua of dP_3 in *N. matrix* and *G. bilamina* but which is also present on dP_3 in undescribed Riversleigh balbarines referable to *Nambaroo* and in which there is also considerable abbreviation of the protolophid (pers. obs.). Ride (1971) suggested that close proximity of the protoconid and metaconid on dP_3 is plesiomorphic for macropodoids (his macropodids), and the protostylid or its reduced form of a protostylid crest in both potoroids and macropodids suggests that this character is similarly plesiomorphic.

While lower molar morphologies in *G. bilamina* and *Dorcopsoides* are similar in many respects, they differ markedly in that *Dorcopsoides* has a well-developed posterior cingulid, absent in all bulungamayines but present in balbarines. Derivation of *Dorcopsoides* from a bulungamayine ancestor would require development of a neomorphic posterior cingulid, such development possibly indicated by the swollen hypolophid base of *Hadronomus*. Evolution from a balbarine ancestor would require modification to both the anterior cingulid and compressed protolophid of M_1, but modification of pre-existing structures is a more usual evolutionary phenomenon than the development of new structures. This notwithstanding, dental morphology in bulungamayines is such that, on

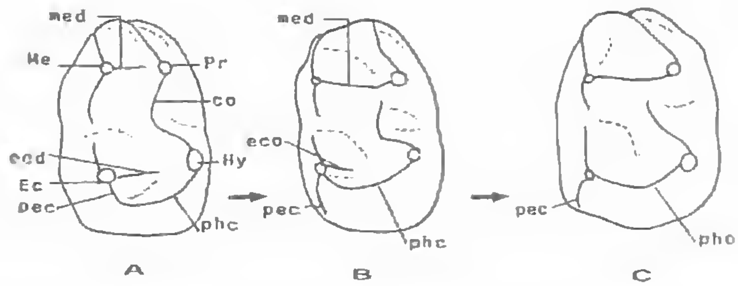

FIG. 4. Development of lophodonty in bulungamayines, illustrated by RM_1. A, *Nowidgee matrix* . B, equivalent to *B. delicata*. C, *G. bilamina*. Abbreviations: Pr=protoconid, Me=metaconid, med=metacristid. HY=hypoconid, Ec=entoconid, ecd=buccal crest from entoconid, phc=posthypocristid, pec=postentocristid, co=cristid obliqua.

the grounds of parsimony, they, rather than balbarines, must be preferred as the group most closely ancestral to macropodids.

In the hypothesis of molar evolution within Bulungamayinae advanced herein, there is a transition from a potoroid-like molar in basal species to a macropodid-like molar in derived species. Such a transitional sequence within the group may explain the differing views of familial affinity of bulungamayines (Case, 1984; Woodburne, 1984; Flannery et al., 1984). At the time their respective views were advanced, only 2 bulungamayine species, *B. delicata* and *W. naughtoni*, had been described. Molar morphology in both those species is intermediate in the transitional sequence and it is not surprising that both macropodid and potoroid affinities could be argued on the basis of these species.

If, as seems likely from the evidence provided herein, that bulungamayines are directly ancestral to macropodids, then monophyly of Bulungamayinae cannot be stated with certainty. Further doubts also arise concerning monophyly of Macropodidae.

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